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Characterization of the Plant–Soil feedback index in alpine meadow degradation and recovery: A field experiment

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Most plant–soil feedback studies have been conducted on the mechanism by which soil directly influences plant growth performance and mostly in indoor pot experiments; however, it is unclear how plant–soil feedback is influenced by plant, soil and microbial diversity in grassland ecosystems in alpine meadows with high plant diversity. In this study, plant–soil feedback patterns were investigated by analyzing plant, soil and microbial characteristics across seven gradients in the time series from light degradation to 10-years of recovery, classified into three categories: ecosystem multifunctionality, biotic and abiotic factors, and comparing the strength and magnitude of plant–soil feedback in alpine meadows of degradation stages and years of recovery. The results showed that the plant-soil feedback relationships in alpine meadows differed significantly in three aspects: ecosystem multifunctionality, biotic and abiotic factors in the degradation stage and recovery years, and under the degradation gradient, ecosystem multifunctionality decreased from 0.34 to −0.99 with the deepening of degradation, biotic factors increased from −0.17 to 0.09, and abiotic factors increased from −0.17 to 0.15, while in the recovery gradient, ecosystem multifunctionality showed a trend of increasing and then decreasing with increasing recovery years, while biotic and abiotic factors showed fluctuating changes. The plant-soil feedback index indicated that the strength and direction of plant-soil interactions during degradation and recovery were different, and the positive feedback effect was 0.34 and 0.38 in the early stage of degradation and recovery, respectively, which were greater than the negative feedback effect. With the deepening of degradation, the negative feedback effect became more and more obvious, and at the stage of extreme degradation, the negative feedback effect reached −0.99, which was much larger than the positive feedback effect. However, with the increase of the recovery years, the positive feedback effect gradually weakened, and finally all of them were negative feedback effects at 10-years of recovery. This study provides a scientific basis for understanding plant-soil feedback in alpine meadow ecosystems and indicates the direction for the next scientific recovery of alpine meadows.

KEYWORDS

plant-soil feedback, ecosystem multifunctionality, biotic factors, abiotic factors, degradation, recovery

1 Introduction

Plant communities change the soil community structure, and this change in turn influences the growth rate of the plant communities (Bever et al., 1997). Soil organisms can strongly affect the establishment of plant diversity as well as the direction of community succession in grassland wastelands and abandoned arable land (Bever, 2003). Soil organisms can mediate these interactions by directly promoting or inhibiting plant growth or by influencing predation or nutrient availability (Wardle et al., 2004); these interactions are referred to as plant–soil feedback (Chen et al., 2022). Plant–soil feedback contributed to the succession of plant communities, the invasiveness of alien species and the coexistence of different species within the community (Van der Putten et al., 1993; Klironomos, 2002; Ehrenfeld et al., 2005; Lee et al., 2012). In addition, changes in intensity and direction can shift plant community dynamics from a state of coexistence between different species to one of successional competition, which plays a positive role in maintaining the stability of ecosystem structure and function (Hector and Bagchi, 2007; Gamfeldt et al., 2008). Thus, interactions between plants and soil biotic and abiotic properties can effectively explain structural differences plant communities on aboveground, as well as the extent to which ecosystems react to environmental change (Ehrenfeld et al., 2005; Bardgett and Wardle, 2010).

As a major ecosystem on the Qinghai-Tibet Plateau, alpine meadows play an important role in water conservation, biodiversity maintenance and carbon sequestration (Breidenbach et al., 2022; Sun et al., 2022). However, in recent years, due to climate warming, unreasonable human activities (e.g., overgrazing, grassland reclamation and construction) and destruction by small rodents (mainly plateau pika and plateau zokor), approximately 4.23 × 10^5 km^2 of grassland on the Qinghai-Tibet Plateau has been degraded to varying degrees, with 16.5% of the degraded grassland severely degraded to “black soil banks”. This is a serious threat to the sustainability of alpine meadow ecosystems (Chapin et al., 2000; Dong et al., 2010; Cardinale et al., 2012; Laughlin, 2014), and artificial grassland revegetation is considered to be one of the main effective ways to restore degraded meadows (Shang et al., 2018).

Most plant–soil feedback studies have been conducted mainly in grasslands and tropical forests, with the main findings being negative feedback effects of plant species on their conspecifics (Kulmatiski et al., 2008; Petermann et al., 2008; Mangan et al., 2010). However, there are few studies on the differences in plant–soil feedback during alpine meadow degradation and recovery based on field experiments. Current research on plant–soil feedback is dominated by controlled field and indoor trials (Bickford et al., 2022; Buchenau et al., 2022; Dan et al., 2022; Dudenhöffer et al., 2022; Huberty et al., 2022), which validate the effects of plant–soil feedback mechanisms on population dynamics and community composition, and these studies have provided insight into the important role of plant–soil feedback mechanisms in community development (Kulmatiski et al., 2006). However, most studies on plant–soil feedback relationships have focused on the individual species level, and fewer study have been conducted at the community level, limiting our understanding of plant–soil feedback during community-based alpine meadow degradation and recovery (De Deyn et al., 2004; Kardol et al., 2006; Kulmatiski et al., 2006). In addition, controlled indoor experiments do not well reproduce the natural environment in which alpine meadow ecosystems are found, and plant–soil feedback still need to be studied in the natural environment and at longer time scales (Liu et al., 2014; Wang et al., 2022). Negative plant–soil feedback plays a major role in maintaining plant species diversity, while positive plant–soil feedback may lead to community convergence (Bever, 2003; Bever et al., 2010). However, we lack a clear understanding of the mechanism of plant–soil feedback. Especially in the context of global environmental changes, in the wild natural environment of the widespread alpine meadow ecosystem, plant–soil feedback interacts with other known effects to influence plant community composition and ecosystem versatility. Solving these problems will contribute to the prediction of plant–soil feedback in the wild environment.

Therefore, this study took grassland under different degradation gradients and different recovery years in Maqin County as the research object. By analyzing the changes in plant, soil and microbial characteristics in different degradation stages and different recovery years, the characteristics of plant, soil and microbial community diversity in the process of degradation and recovery were quantified, and the occurrence rules in different degradation stages and different recovery years were determined. The feedback relationship between plants and soil was studied, and the interaction mechanism of the plant–soil relationship was revealed, which provided a theoretical basis and scientific reference for the recovery of alpine meadow ecosystems.

2 Materials and methods

2.1 Sample site overview

The experimental area is located in Jun Ranch of Sanjiangyuan Alpine Meadow Research Observatory (Jun Ranch, Machin County, Golog Tibetan Autonomous

TABLE 1 Criteria for evaluating degraded grassland.

Degradation gradients	Vegetation coverage (%)	Proportion of grass production (%)	Proportion of edible forage (%)	Change in height of edible forage (cm)	Pasture quality
Primary vegetation	80–90	100	70	25	Standard
Slight degradation	70–85	50–75	50–70	Drop 3–5	Drop 1 level
Moderate degradation	50–70	30–50	30–50	Drop 5–10	Drop 1 level
High degradation	30–50	15–30	15–30	Drop 10–15	Drop 1–2 level
Severe degradation	<30	<15	Nearly 0	~	Very poor

TABLE 2 The basic information of the experimental plots.

Treatment	Experiment	Latitude/ Longitude	Altitude/ m	Vegetation composition
D1	Slight degradation	34°21′18″N100°28′54″E	3940	*Kobresia pygmaea* C. B. Clarke, *Kobresia humilis* Sergievskaya., *Kobresia capillifolia* C. B. Clarke, *Poa crymophila* Keng, *Carex atrofusca Schkuhr* subsp, *Potentilla anserina* var. nuda and *Polygonum viviparum* L
D2	Moderate degradation	34°31′44″N100°57′77″E	4106	*Kobresia pygmaea* C. B. Clarke, *Kobresia humilis* Sergievskaya., *Kobresia capillifolia* C. B. Clarke, *Poa crymophila* Keng, *Carex atrofusca Schkuhr* subsp, *Potentilla nivea* L.,*Leontopodium hayachinense* Hara et Kitam. and *Saussurea pulchra* Lipsch
D3	High degradation	34°21′17″N100°28′47″E	3,950	*Potentilla nivea* L, *Ajania tenuifolia* (Jacq.) Tzvel., *Herb of Tibet Lancea*, Tibet Lancea, *Ajuga lupulina* Maxim., Saussurea pulchra Lipsch., *Aster tataricus* L. f. and *Thalictrum aquilegiifolium* var. *sibiricum* Linnaeus
D4	Severe degradation	34°26′24″N100°19′12″E	3797	*Aconitum Pendulum* Busch, *Morina chinensis* Diels, *Pedicularis kansuensis* Maxim, *Ligularia virgaurea* Matt and *Artemisia hedinii* Ostenf. et Pauls
R1	1-year-old artificial grassland	34°23′24″N100°17′24″E	3791	*Elymus nutans, Festuca sinensis* and *Poa crymophila*
R5	5-year-old artificial grassland	34°28′12″N100°10′47″E	3,787	*Elymus nutans, Festuca sinensis* and *Poa crymophila*
R10	10-year-old artificial grassland	34°25′48″N100°15′36″E	3,759	*Elymus nutans, Festuca sinensis* and *Poa crymophila*

Prefecture, Qinghai Province, 34°22′-34°20′N, 100°30′-100°29′E), at an altitude of 3,783.5 m. It is a continental semihumid climate type on the Qinghai-Tibet Plateau, with an average annual temperature of -5.6–3.8°C, with an average temperature of −12.6°C in January and 9.7°C in July. The average annual precipitation is 500–600 mm, and the annual evaporation is relatively large, generally 730–1700 mm. There is no absolute frost-free period, and the forage grows for approximately 150 days. The soil type is alpine meadow soil, and the grass type is alpine meadow. The vegetation types are *Kobresia pygmaea* C. B. Clarke and *K. humilis* Sergievskaya. and *K. capillifolia* C. B. Clarke as the dominant species and *Poa crymophila* Keng, *Carex atrofusca Schkuhr* subsp, and *Polygonum viviparum* L as companion species in alpine meadows. Due to climate change, human activities and rodent feeding activities, the alpine meadow has been degraded to alpine meadow with *Aconitum* pendulum busch, *Morina chinensis* Diels, *Pedicularis kansuensis* Maxim and *Ligularia virgaurea* Mattf, and *Artemisia hedinii* Ostenf. et Pauls, were the dominant severely degraded meadows.

2.2 Sample selection

In August 2020, an experimental plot was selected in the Military Pasture of Sanjiangyuan Alpine Meadow Research and Observation Station. According to the ‘Grading Standard of Natural Grassland Degradation, Desertification and Salinization’ (GB19377-2003) and the classification standard of Ma et al. (2002) (Table 1), the method and principle of temporal succession were replaced by spatial sequence. The meadows with basically the same climate and soil conditions

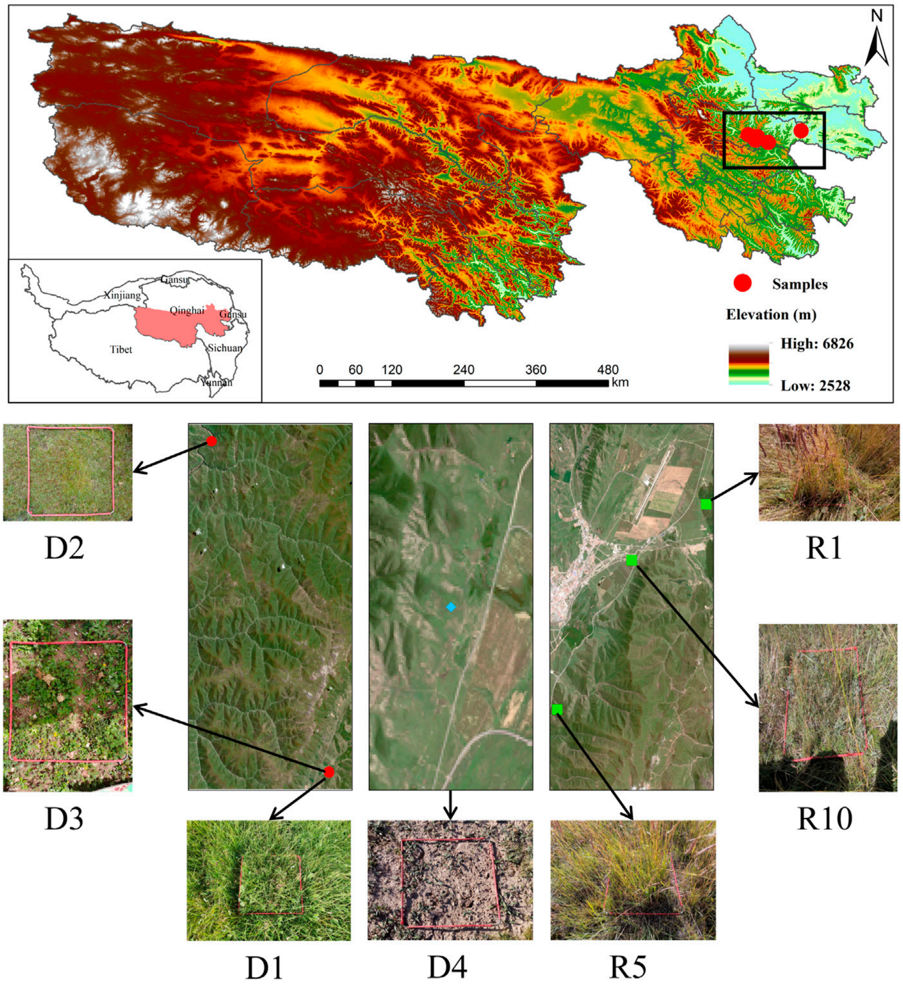

FIGURE 1
Schematic diagram of the location of the study area.

in the study area were divided into slightly degraded alpine meadow (D1), moderately degraded alpine meadow (D2), highly degraded alpine meadow (D3) and severely degraded alpine meadow (D4) (She et al., 2021) (Table 2). The plots with different recovery years were compared with the severely degraded meadow, and the native vegetation was sparse in the severely degraded stage. The vegetation was low or dead, the soil surface was exposed in patches, poisonous weeds were overgrown and spread, and the grazing value basically disappeared. Before the establishment of artificial grassland, it was a typical severely degraded grassland. The dominant species of Cyperaceae were replaced by poisonous weeds, and the coverage of native vegetation was less than 10%. The vegetation is composed of *A. pendulum, Potentilla chinensis, Ligularia virgaurea, P. resupinata,* and *Ajania tenuifolia*. In 2019, 2015 and 2010, perennial artificial grasslands dominated by *Elymus nutans, Festuca sinensis* and *P. crymophila* were replanted on severely degraded grassland. The seeds of *Elymus nutans, Festuca chinensis* and *P. crymophila* used in the artificial grassland were produced by the local grass seed breeding farm with a sowing rate of 37.5 kg/hm^2 and a sowing rate of 3:1:1, and the amount of fertilizer applied was 45 kg/hm^2 (diammonium hydrogen phosphate compound fertilizer). The sowing distance was 20 cm, and the agronomic measures were as follows: deep turning-raking-fertilizing-sowing-covering-soil-compacting-fencing. Each sample plot was 20 hm^2, and each treatment had 5 replicates. The management measures after planting were fencing and culturing, without livestock grazing disturbance factors. In August 2020, severely degraded alpine meadow (D4), artificial grassland established in 2019 (1-year-old artificial grassland, 1AG, R1), artificial grassland established in 2015 (5-year-old artificial grassland, 5AG, R5), and artificial grassland established in 2010 (10-year-old artificial grassland, 10AG, R10) were tested (Figure 1; Table 2).

2.3 Plant and soil sample collection

Five randomly set 50 cm × 50 cm samples were set in each sample plot for the vegetation community survey. To avoid edge effects, the interval between each sample square should not be less than 10 m. The vegetation sample survey mainly included the survey of overall community characteristics, including meadow health, dominant species, number of species, total cover, average plant height (multiple replicates to take the average value), and the survey of species characteristics, including the subcoverage of each species, number of plants (multiple degrees), plant height and so on. The average height of the community in the sample square was recorded with a tape measure, and then the total cover of the community in the sample square was measured by visual inspection, followed by measuring the height of a single species in the sample square with a tape measure (5 replicates, less than 5 plants were all measured), measured the cover of a single species by visual estimation, and calculating the multiplicity of species. Afterwards, the plants in the sample plots were cut in flush ground and put into envelopes, brought back to the laboratory and dried at 65°C for constant weight, then weighed and recorded.

After taking the plant samples, the underground parts of the plants were collected in the sample cubes using the soil column method (*Φ* = 50 mm). Three augers were taken for each sample cube, and each auger was divided into 3 layers of 10 cm soil columns each (0–10, 10–20, 20–30 cm), and the soil samples were sieved with a mesh of 5 mesh. After rinsing the soil with adequate water, the live roots were picked out according to the flexibility of the root system and the color of the cross-section. Finally, washed live root systems were put into large envelopes, dried in an oven at 65°C for constant weight and then weighed. Soil samples from the 0–30 cm soil layers were passed through a 2 mm sieves to remove debris and used for soil property determination. Soil microorganisms were obtained by the X-type five-point method, and soil samples 0–10 cm were taken. All samples were collected in sterilized self-sealing bags, stored frozen and shipped back to the laboratory in time. Ten grams of fresh soil was stored at −80°C in the refrigerator for DNA extraction and high-throughput sequencing. Sample sequencing was performed at Majorbio Cloud platform (http://www.majorbio.com/).

2.4 Indicator determination and methods

2.4.1 Calculation of plant species diversity

In community analysis, the importance value (IV) can be used as a measure of plant species dominance. The relative coverage (RC), relative height (RH) and relative abundance (RA) of individual species were used to calculate the important values of each species:

RC (%) = The coverage of a species/coverage of all species
RH (%) = the height of the individual species/the sum of the individual heights of all species
RA (%) = Species of number of individuals/number of individuals of all species

$$IV = (RC + RH + RA)/3$$

The Patrick richness, Shannon–Wiener diversity, Pielou evenness and Simpson dominance index were used to calculate the species diversity:

Patrick richness index (R)

$$R = S$$

Shannon–Wiener diversity index (H)

$$P_i = \frac{IV_i}{IV_{Total}}$$

$$H = -\sum_{i=1}^{S} (P_i \ln P_i)$$

Pielou evenness index (E)

$$E = \frac{H}{\ln s}$$

Simpson dominance index (D)

$$D = 1 - \sum_{i=1}^{S} P_i^2$$

where s is the sum of all the plant species in the sample box, i is the plant species in the sample box, and P_i is the relative importance of the I species.

2.4.2 Soil physical and chemical property determination method

The total nitrogen content was determined by the Kjeldahl method, total phosphorus was determined by the sodium hydroxide alkali fusion-mo-sb anti-colorimetric method, total potassium was determined by the sodium hydroxide alkali fusion-flame photometry method, available nitrogen was determined by the sodium hydroxide alkali decomposition-diffusion method, available phosphorus was determined by the sodium bicarbonate leaching-molybdoantimony colorimetric method, available potassium was determined by the ammonium acetate leaching-flame photometric method, and soil organic matter was determined by the potassium dichromate volumetric method-external heating method. The soil organic carbon content was determined by heating with potassium dichromate acid, the soil water content was measured by drying and weighing, the soil pH was determined by the potentiometric method, and the soil bulk density was determined by the ring knife method. Refer to "Soil Agrochemical Analysis" for specific measurement methods (Bao, 2000).

10.3389/fenvs.2022.1097030

TABLE 3 Plant–soil feedback index system.

Primary indicator	Secondary indicator	Indicator interpretation
Ecosystem Multifuctionality	Soil Nutrient	1.Total Nitrogen
		2.Total Phosphorus
		3.Total Potassium
		4.Available Nitrogen
		5.Available Phosphorus
		6.Available Potassium
		7.Organic Matter
		8.Organic Carbon
	Biomass	9.Aboveground Biomass
		10.Belowground Biomass
Biotic Factors	Aboveground Biodiversity	1.Species Richness
		2.Shannon Wiener Diversity Index
		3.Evenness Index
		4.Simpson Diversity Index
	Underground Biodiversity	5.Bacteria-Shannon Index
		6.Bacteria-Chao Index
		7.Bacteria-Simpson Index
		8.Bacteria-ACE Index
		9.Fungi-Shannon Index
		10.Fungi-Chao Index
		11.Fungi-Simpson Index
		12.Fungi-ACE Index
Abiotic Factors	Other Soil Properties	1.Soil Moisture
		2.Soil pH
		3.Soil Bulk Density

2.5 Calculation of plant–soil feedback indices

2.5.1 Plant–soil feedback index system

The data of this study involved two sequences, namely, plant and soil characteristics at different stages of degradation (D1, D2, D3 and D4) and at different years of recovery (D4, R1, R5 and R10). The 10 indicators involved in ecosystem multifunctionality (soil nutrients, aboveground biomass, belowground biomass), 12 indicators involved in biotic factors (aboveground biodiversity and belowground biodiversity) and 3 indicators involved in abiotic factors (soil water content, soil pH and soil capacity) were transformed into 3 composite indicators using factor analysis corresponding to different stages of degradation and different stages of recovery years. Three indicators were transformed into three composite indicators (Table 3).

2.5.2 Model selection

Factor analysis is an approach for studying the internal dependencies of the correlation matrix between multiple variables to identify several random factors that combine key information about all variables and represent the underlying structure of the data. The factors being measured are uncorrelated with each other, and all variables can be represented as linear combinations of common factors. Taking n samples, p indicators and X = (X1, X2..., XP) as random variables, the model expression is reproduced below.

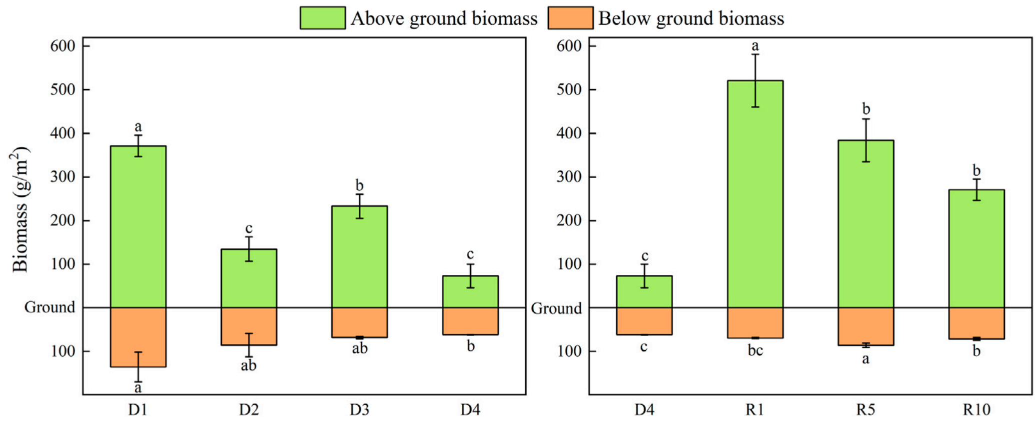

FIGURE 2
Changes in plant biomass at different stages of degradation and at different recovery years.

$$X_1 = a_{11}F_1 + a_{12}F_2 + \cdots + a_{1m}F_m + \mu_1$$
$$X_2 = a_{21}F_1 + a_{22}F_2 + \cdots + a_{2m}F_m + \mu_2$$
$$\cdots$$
$$X_p = a_{p1}F_1 + a_{p2}F_2 + \cdots + a_{pm}F_m + \mu_p$$

where the matrix A = (aij) is called the factor loading matrix, aij is the factor loading and μ is the special factor representing the variance of the variables that cannot be explained by the common factor and can be ignored in the actual analysis. In the operation process, factor analysis was performed on the variable data set using econometric statistical analysis software, and the combined scores of the factors were finally determined by testing Bartlett's spherical and Kaiser-Keyer-Olkin statistics of the samples and measuring the main factors using the maximum variance method of rotation.

2.5.3 Model selection

The feedback effect index (FI) between plants and soil, if FI > 0, is a positive feedback effect; if FI < 0, it shows a negative feedback effect. The specific calculation formula is as follows.

$$FI = In(X/X0)$$

where X is the target treatment group index and X0 is the average of all treatment group indices (Pernilla Brinkman et al., 2010; Jing et al., 2015).

3 Results

3.1 Characteristics of grassland plants under different degradation gradients and different recovery durations

3.1.1 Biomass

During the degradation of alpine meadows, total aboveground biomass showed a significant decrease ($p < 0.05$), and belowground biomass showed a decreasing trend. Aboveground biomass of the artificial meadows was significantly higher than that of the severely degraded ones, but the difference between the aboveground biomass of the artificial meadows restored for 5 and 10 years was not significant compared with that of the artificial meadows restored for 10 years. Belowground biomass of artificial grassland showed a trend of increasing and then decreasing with increasing recovery years ($p < 0.05$), and the difference was not significant when compared with the severely degraded artificial grassland at 1 year of recovery. The establishment of artificial grassland led to an increase in aboveground biomass, which had little effect on belowground biomass, but both aboveground and belowground biomass tended to decrease with increasing years (Figure 2). During the degradation of alpine meadows, the biomass of functional groups evolved from mainly Gramineae and Sedge to mainly Compositae and Forbs, the biomass of Gramineae was the lowest in D2 and D4, and was 0 in D4, the biomass of Sedge showed a gradually decreasing trend, the biomass of Compositae showed a gradually increasing trend up to D3, and decreased in D4, the biomass of Forbs decreased in D2 and D4, and decreased to The biomass of weed species decreased in D2 and D4, and decreased to the lowest in D4. The plant community structure was changed by the establishment of artificial grassland. The dominant species in the D4 was mainly Compositae, while the dominant species in artificial grassland was mainly Gramineae. The dominant species in the 1-year-old artificial grassland was *Elymus nutans*, the dominant species in the 5-year-old artificial grassland was *Elymus nutans* and *K. humilis*, and the dominant species in the 10-year-old artificial grassland decreased, and the species dominated by Compositae started to gain the subdominant species status. The dominance of grass dominated by *Elymus nutans* gradually decreased with the extension of the establishment period (Figure 3).

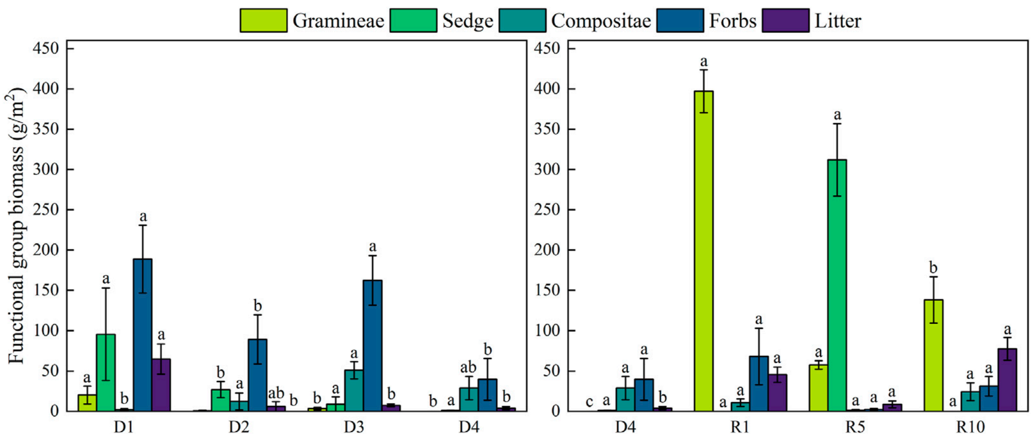

FIGURE 3
Changes in functional group biomass at different degradation stages and recovery years.

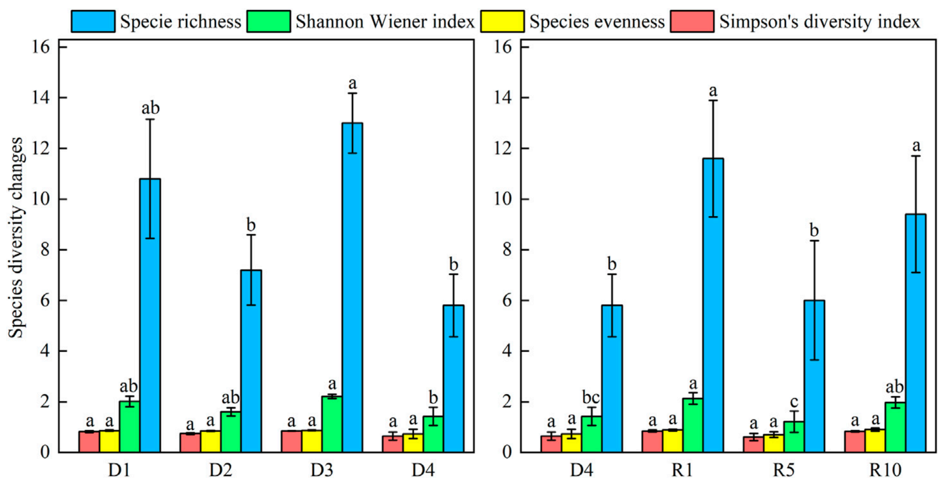

FIGURE 4
Changes in the species diversity of plant communities at different degradation stages and different recovery durations. Note: Different lowercase letters represent significant differences in species richness, Shannon–Wiener index, species evenness index and Simpson diversity index between different degradation stages and recovery years (p < 0.05).

3.1.2 Aboveground species diversity

Plant species diversity indices of the plant communities all showed a decreasing trend. Species richness and the Shannon-Weiner diversity index reached the highest at D3, and species richness was significantly different from D2 and D4 ($p < 0.05$) and not significantly different from D1, unlike the Shannon–Wiener index D4, which was significantly different from D1, D2, and D3, while there was no significant difference between the first three stages. Neither the uniformity index nor the Simpson index from D1 to D4 was significant ($p > 0.05$), but both showed the lowest values at D4. Species richness was significantly higher ($p < 0.05$) in the artificial grassland restored for 1 year and 10 years than in the severely degraded grassland and restored for 5 years. The Shannon-Weiner diversity index was higher in the artificial grassland restored for 1 year than in the severely degraded, restored for 5 years and restored for 10 years ($p < 0.05$). Differences in evenness index and Simpson's diversity index between artificial grassland and severely degraded grassland were not significant (Figure 4).

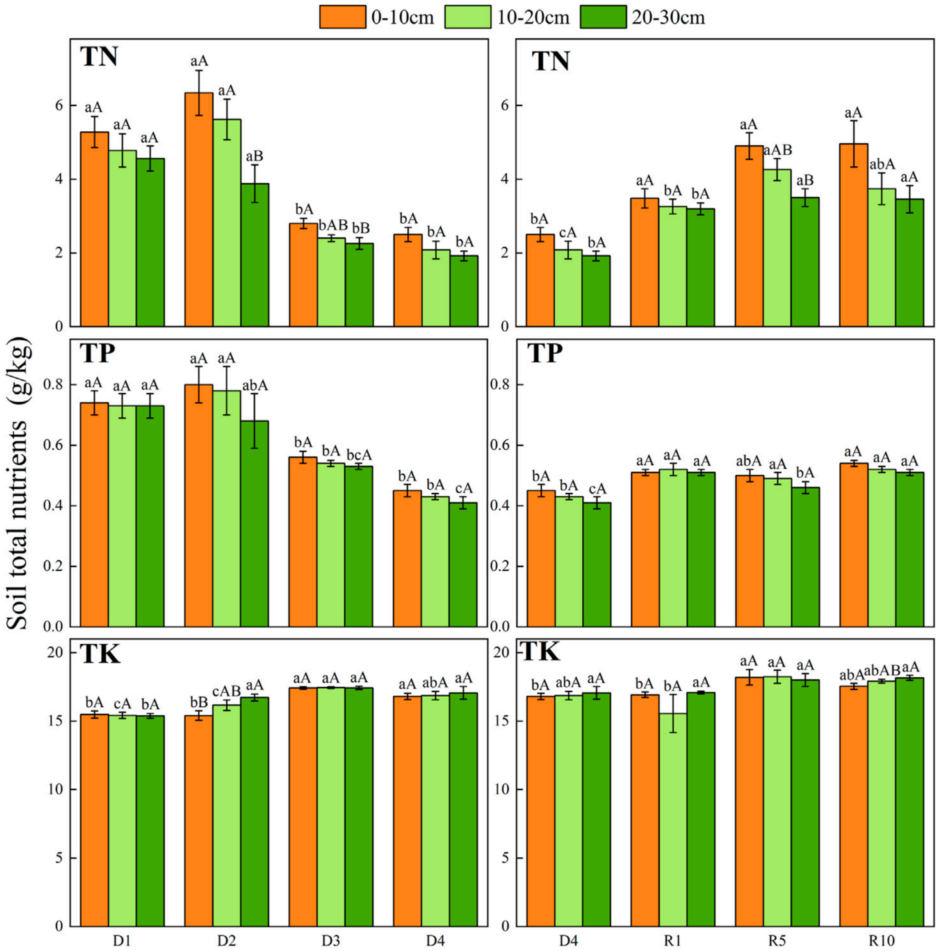

FIGURE 5
Changes in total soil nutrients under different soil layers at different degradation stages and recovery years.

3.2 Soil characteristics of grassland under different degradation gradients and different recovery durations

3.2.1 Soil nutrients

From D1 to D4, the contents of TN and TP in the 0–10 cm surface soil were higher than those in 10–20 cm and 20–30 cm. From D1 to D4, TN and TP showed a gradually decreasing trend but slightly increased in the D2 stage. There was no significant change in TK content from D1 to D4, and TK showed an increasing tendency in D3 compared with severe degradation. Total nutrients (total N, P and K) in artificial grassland increased with the increase in the recovery years, but there was no significant difference between soil layers (Figure 5).

From D1 to D4, the AN, AP, and AK contents in the 0–10 cm surface soil were higher than those in the 10–20 cm and 20–30 cm soil layers, especially AK in the 0–10 cm soil layer. From D1 to D4, AN, AP, and AK showed a gradually decreasing trend but slightly increased in the D2 stage. From D1 to D4, there was no significant change in AK content, and AK showed an increasing tendency in both D2 and D3. Compared with severe degradation, the available nutrients (available N, P and K) of artificial grassland decreased with increasing recovery years, the available N, P and K of artificial grassland restored for 10 years differed significantly between different soil layers, and the content of available nutrients decreased gradually with the deepening of soil layers ($p < 0.05$) (Figure 6).

From D1 to D4, the content of SOC in the top layer of 0–10 cm soil was higher than those in 10–20 cm and 20–30 cm, especially in the 0–10 cm layer. Compared with severe degradation, the soil organic carbon of artificial grassland increased ($p < 0.05$), but with the extension of the recovery period, a "V"-shaped trend was observed in recovery year 1, recovery year 5 and recovery year 10, the lowest in recovery year 5 (Figure 7).

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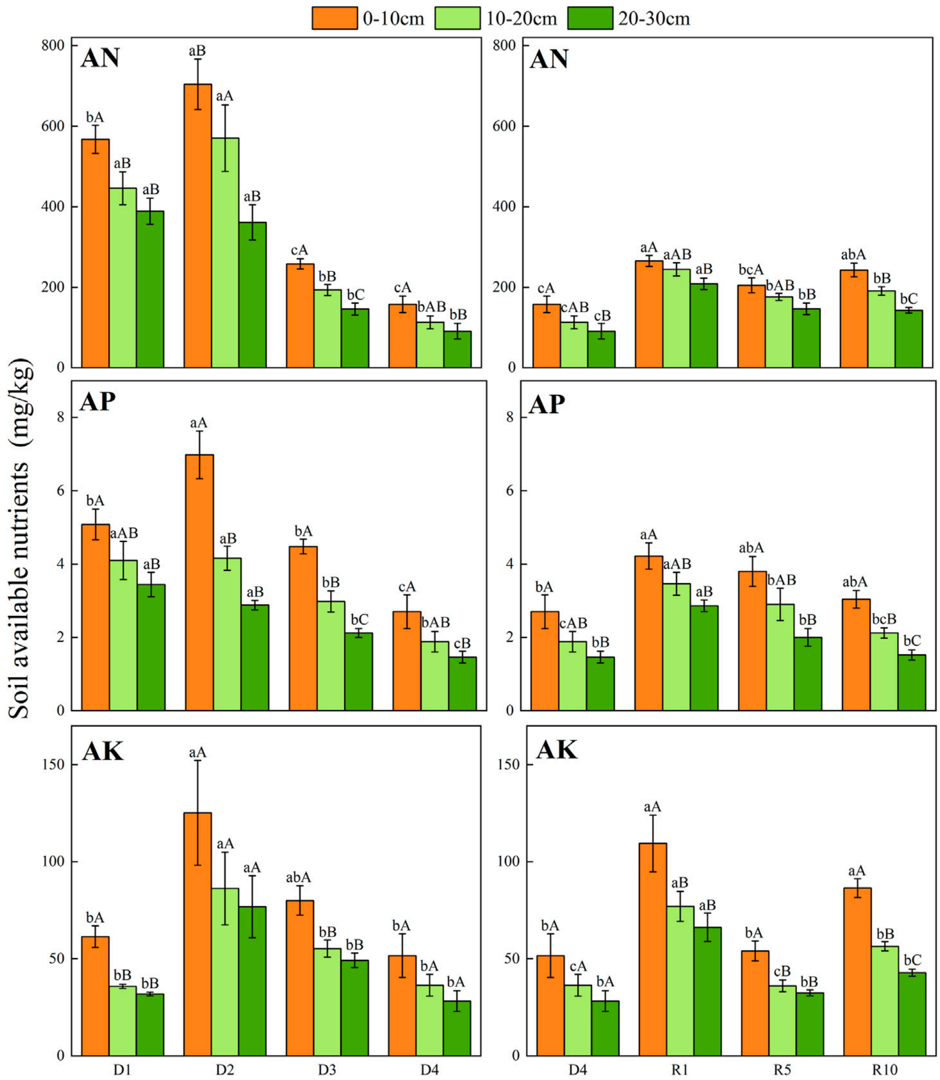

FIGURE 6
Changes in soil available nutrients in different soil layers at different degradation stages and recovery years.

3.2.2 Other soil properties

The soil bulk density increased during the process from D1 to D4, while the soil water content gradually decreased. Soil bulk density was highest in the process of recovery in severe degradation and lowest in artificial grassland in 1 year of recovery and gradually increased with the recovery years. The severe degradation of the soil water content increased compared with that of the artificial grassland, but with the increase in recovery years, the soil water content basically did not change (Figure 8).

The pH increased from D1 to D4. During the recovery process, the soil pH was highest in the same soil layer with severe degradation, lowest in the artificial grass by 1 year of recovery, and gradually increased as the recovery years progressed (Figure 9).

3.3 Microbial characteristics of meadows under different degradation gradients and different recovery durations

The alpha diversity of bacterial and fungal communities showed opposite trends between degradation and recovery processes (Table 4). The Shannon and Chao indices of bacteria and fungi increased significantly with increasing degradation, the Chao indices of fungi were in the order of D4 (697.1) > D3 (660.5) > D2 (643.3) > D1 (443.7). In contrast, the fungal Shannon and Chao indices of the recovery process were significantly lower ($p < 0.05$) from R5 to R10. The bacterial Chao index showed a similar trend, while the bacterial Shannon index did not differ significantly between the different recovery years. The Simpson diversity index of bacteria was

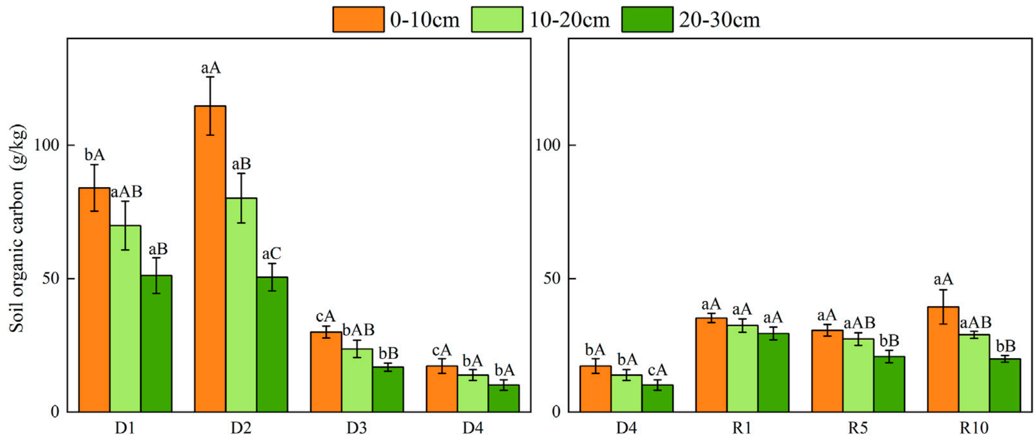

FIGURE 7
Changes in soil organic carbon under different soil layers at different degradation stages and recovery years.

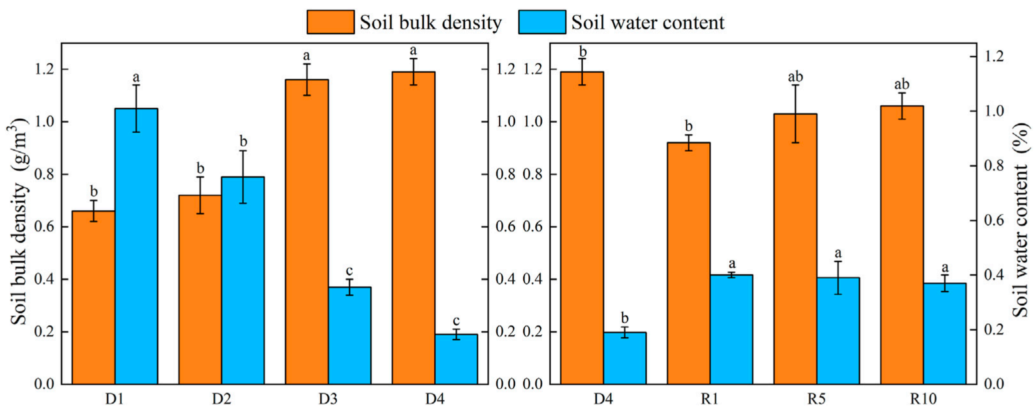

FIGURE 8
Changes in soil bulk density and soil water content under different soil layers at different degradation stages and recovery years.

significantly different ($p < 0.05$) between the highly and severely degraded stages of degradation, while there was no significant difference between the recovery years, and the Simpson diversity index of fungi was not significantly different between degradation stages and recovery years. The ACE diversity index of bacterial and fungal communities showed no significant patterns during either degradation or recovery.

3.4 Grassland plant–soil feedback relationships at different degradation gradients and different recovery years

Indicators incorporated in ecosystem multifunctionality are all quantitative indicators of soil nutrient cycling, nutrient pool accumulation and good above- and belowground productivity, where nitrogen and phosphorus are key factors for ecosystem production and biomass are proxies for good grassland productivity. In light and moderate degradation stages, alpine meadow degradation has a positive plant–soil feedback effect on ecosystem multifunctionality and reaches its maximum at moderate degradation; in the high and severe degradation stages, alpine meadow degradation has a negative plant–soil feedback effect on ecosystem multifunctionality and reaches its maximum by severe degradation. In different stages of alpine meadow degradation, the plant–soil feedback on ecosystem multifunctionality changed to negative feedback after reaching the maximum in moderate degradation. Negative plant–soil feedback of alpine meadow degradation on biological factors was observed in mild degradation, and

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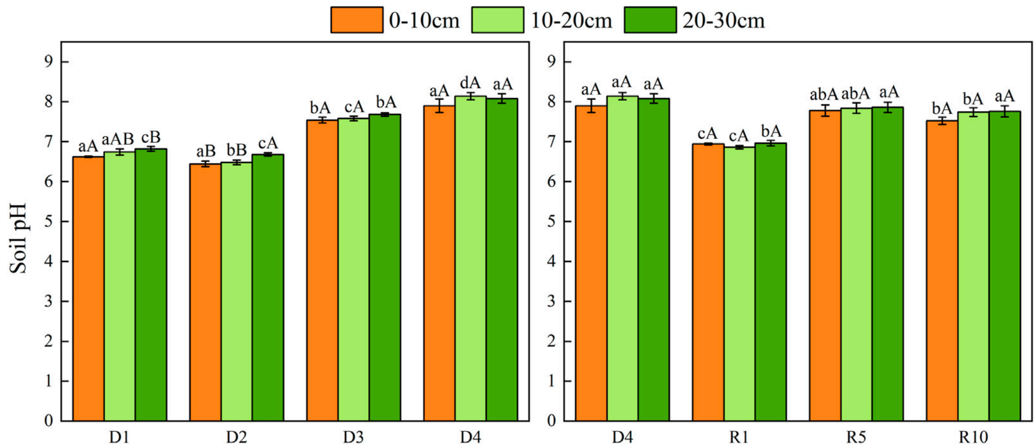

FIGURE 9
Changes in soil pH under different soil layers at different degradation stages and recovery years.

TABLE 4 Community diversity of bacteria and fungi at different stages of degradation stages and recovery years.

	Treatment	Shannon	Chao	Simpson (%)	ACE
Bacteria	D1	6.40 ± 0.07c	2521.10 ± 54.46b	0.51 ± 0.00a	2482.40 ± 53.18b
	D2	6.60 ± 0.04b	2945.78 ± 80.92a	0.36 ± 0.00 ab	2936.38 ± 82.78a
	D3	6.71 ± 0.04ab	2924.23 ± 68.72a	0.30 ± 0.00b	2931.06 ± 67.69a
	D4	6.77 ± 0.01a	3107.03 ± 69.38a	0.29 ± 0.00b	3090.46 ± 75.83a
	R1	6.60 ± 0.06a	2945.45 ± 57.87b	0.42 ± 0.00a	2905.85 ± 47.60b
	R5	6.73 ± 0.05a	3130.35 ± 43.99a	0.34 ± 0.00a	3139.40 ± 47.57a
	R10	6.64 ± 0.03a	2906.09 ± 36.91b	0.33 ± 0.00a	2871.58 ± 27.53b
Fungi	D1	3.05 ± 0.16b	443.74 ± 33.81b	12.18 ± 0.01a	450.13 ± 32.38a
	D2	3.36 ± 0.54ab	643.34 ± 106.37a	13.06 ± 0.08a	632.00 ± 103.92ab
	D3	4.25 ± 0.08a	660.49 ± 31.68a	3.46 ± 0.00a	652.66 ± 31.77b
	D4	3.92 ± 0.29ab	697.05 ± 39.04a	6.18 ± 0.02a	691.79 ± 36.70b
	R1	4.09 ± 0.03a	612.96 ± 32.23ab	3.65 ± 0.00a	610.77 ± 30.58a
	R5	4.04 ± 0.10a	685.43 ± 32.45a	6.91 ± 0.02a	676.90 ± 32.44a
	R10	2.79 ± 0.65b	502.24 ± 44.04b	25.70 ± 0.12a	503.15 ± 34.42b

positive plant–soil feedback was observed from moderate degradation to severe degradation, which showed a tendency to increase with the degradation degree. In the early stage of the degradation process, alpine meadow degradation has a negative plant–soil feedback effect on abiotic factors; the heavy and severe degradation stages, alpine meadow degradation has a positive plant–soil feedback effect on abiotic factors, and it shows a trend of increasing gradually. It can be seen that at the stage of severe degradation, planted artificial meadow has a negative plant–soil feedback effect on ecosystem multifunctionality, and at 1 and 5 years of recovery, planted artificial meadow has a positive plant–soil feedback effect on ecosystem multifunctionality, and it reaches the maximum at 1 year of recovery. During the recovery process, plant–soil feedback on ecosystem multifunctionality changed to negative feedback after reaching a maximum at 1 year of recovery. For severe degradation, the

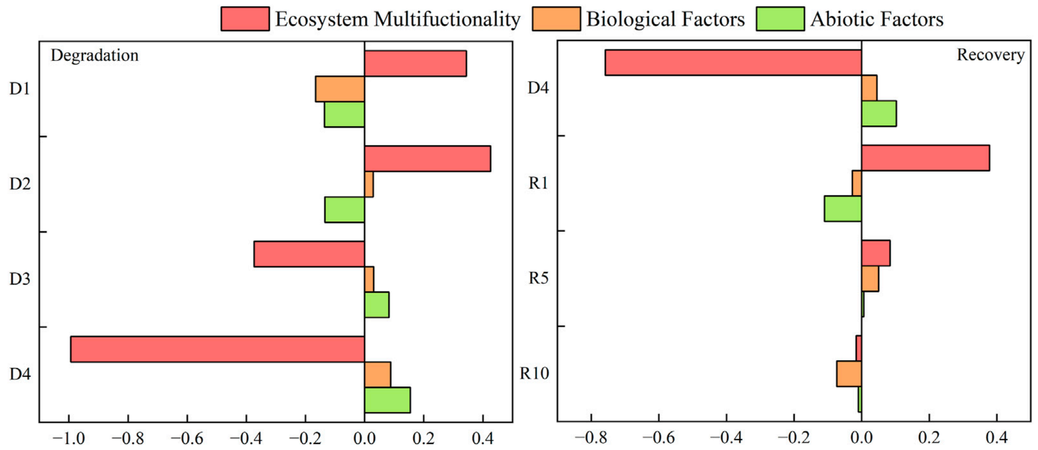

FIGURE 10
Changes in plant–soil feedback index at different degradation stages and recovery years.

constructed artificial grassland had a positive plant–soil feedback effect on biotic factors, negative feedback at 1 year of recovery, positive feedback at 5 years of recovery, and negative feedback at 10 years of recovery, indicating that aboveground community diversity and belowground microbial community diversity were richer at 5 years of artificial grassland than at 1 and 10 years of recovery, and the change pattern of the feedback effect of abiotic factors was consistent (Figure 10).

4 Discussion

4.1 Differences in grassland plant characteristics across degradation gradients and different recovery years

The species diversity index showed an overall decreasing trend from D1 to D4, but a maximum occurred at D3, which is essentially consistent with the findings of this study (Chen et al., 2016; Zhang et al., 2019). The reason for the maximum species diversity in D3 is mainly because the D1 and D2 meadow ecosystems have strong stability, while with the accelerated process of degradation, edible forage grasses decrease, and species such as *Stellera chamaejasme*, *Aconitum pendulum* and *L. virgaurea* begin to occupy the dominant species ecological niche in the community. The increase in the number of species within the community will cause changes in plant community structure and function and will influence the high level of species diversity within the community (Zhou et al., 2012). Disturbances from human activities during the process from D1 to D4 can also have an impact, such as grazing and the survival of rodents in the meadow, cattle, sheep and rodents with foraging preferences, trampling of the meadow during foraging and acts such as seed dispersal as a vector during foraging, which can result in a higher number of species in D3 than in D2 (Wang et al., 2014; Zhang et al., 2021). The species richness and Shannon–Wiener diversity index during meadow degradation showed a unimodal change, with the maximum value being present at D2 (Hao et al., 2020). This study showed no significant difference in species evenness and Simpson's diversity index from D1 to D4, suggesting that anthropogenic disturbance inhibited the dominant species in the community, which provided opportunities for the invasion and expansion of toxic weeds and enhanced the competitiveness of these species to dominate the community, resulting in an increase in the species diversity index, thus indicating that moderate disturbance would improve the species diversity within the community (Zhou et al., 2005; Zhou et al., 2012). The community composition is gradually homogenized, and the species richness and Shannon Weiner diversity index decreased significantly (Zhou, 2001; Jianli et al., 2004; Yuan et al., 2004).

The establishment of artificial grasslands at the stage of severe degradation has a positive effect on long-term recovery of artificial grassland ecosystems (Shang et al., 2018). The establishment of artificial grassland not only improves the productivity of the ecosystem but also corresponds to the introduction of new vegetation and the acquisition of organic matter contributed to the soil system by plant residues and dead leaves, thus improving the structure and function of the soil (Zi et al., 2017; Xing et al., 2020). In this study, plant aboveground biomass showed a decreasing trend with the extension of recovery years, and in the early stage of recovery, competition between species was low, and plants of the grass family were larger and soon occupied a higher ecological position and dominated the whole community, so aboveground biomass was higher (Li et al., 2021). After 5 years of recovery, sedge family plants with low resource requirements gradually increased, and a small number of sedge family plants appeared during the gradual succession of artificial grassland, indicating that the artificial grassland entered the natural recovery process with low weed-like biomass (Zhang et al., 2003). After 10 years of recovery, soil fertility declined, and when nutrients in the soil were insufficient, plants tended to transfer resources to the underground root system to improve the uptake and utilization of limited soil resources, the dominant species status of Gramineae declined, and species dominated by Asteraceae began to be in subdominant species status (Zhang et al., 2012). With the increase in recovery years, all four species diversity indices showed a “V” shape change, which was due to the strong competition of planted species of artificial grassland at the early stage of recovery and their rapid dominance, making the species diversity index decrease; however, with the extension of recovery years, the native species gradually invaded and gained dominance, and the species diversity increased significantly (Wu et al., 2019).

4.2 Differences in soil characteristics of grassland under different degradation gradients and different recovery durations

Soil available potassium, total nitrogen and total potassium showed a decreasing trend as the degradation level increased. There was no significant change in the distribution of soil total potassium content among soil layers in the meadow samples with different degradation levels (Gao et al., 2006). In the same soil layer of different alpine meadow degradation stages, the soil total potassium content varied significantly, and in different soil layers of the same alpine meadow degradation stages, the total potassium content in the same soil layer did not vary significantly (Chen and Zhang, 2013). Soil available nitrogen, available phosphorus and total phosphorus showed an overall decreasing trend but differed in that a small increase was observed at a specific stage. Soil available nitrogen showed a small increase at the stage of severe degradation, and soil available phosphorus showed a small increase at the stage of mild degradation, while soil total phosphorus showed a small increase at the stage of severe degradation. With the intensification of soil degradation, the total phosphorus content of the soil showed a decreasing trend and then an increasing trend, while the available phosphorus content showed a decreasing trend (Zhao et al., 2009). In alpine meadows of the Tibetan Plateau, mineralization of organic nitrogen is the main source of available nitrogen in the soil (Gao, 2007). Plant uptake and natural factors reduce the content of available nitrogen, and effective nitrogen has a small rebound in the process of severe degradation, which may be because the level of severe degradation plant activity is not high, so the amount of uptake is not high, resulting in a small rebound phenomenon. The soil water content showed a decreasing trend with the deepening of degradation (Zhou et al., 2005; Li et al., 2020). The response of alpine meadows to soil at different stages of degradation focuses on soil bulk, and the specific response is expressed as an increase in bulk weight (Zi et al., 2015). Both of these processes reduce the water holding capacity of the soil, leading to a decrease in soil water content (Zhou et al., 2005). At the same time, enhanced evapotranspiration and infiltration also led to the loss of soil water. The loss of soil water in the surface layer of the meadow may be due to evaporation and infiltration from the ground surface, and in the later stages of degradation, the decrease in soil water content decreased (Fan et al., 2019), probably due to low vegetation cover, low plant activity level and reduced transpiration. With the deepening of degradation, the soil capacitance and soil pH showed an increasing trend. Soil pH was higher in the severely degraded stage than in the other degraded stage and showed a decreasing trend from severely degraded to moderately degraded, which was consistent with the integrated results of this study (Gao et al., 2006). Soil organic carbon showed an overall decreasing trend, but a small increase was observed at the stage of severe degradation, and an overall decreasing trend was observed with increasing soil depth, which was consistent with the integration results of this study (Han et al., 2011).

Soil is the most important carrier of nutrient cycling, water balance and microbial activity in terrestrial ecosystems and plays a key role in plant growth, and its physicochemical properties and nutrient status are the most important indicators of ecosystem stability (Liu and Tan, 1994; Yang et al., 2007). Soil nutrients, water content and pH are key indicators for restoring and maintaining the function of damaged ecosystems and play an important role in plant community succession (Li and Ma, 2002; Cheng et al., 2021). In this study, we found that the soil nutrient content in the 0–10 cm soil layer was higher than that in the 10–20 cm and 20–30 cm soil layers, which is due to the short growing season of alpine plants, which are mostly shallow-rooted plants, resulting in shallow root distribution and decomposition of dead roots into organic matter and other nutrients in the soil, which accumulate in the soil surface layer (Yue et al., 2015). Total nitrogen, phosphorus and potassium in artificial grassland showed an increasing trend with the increase in recovery years, but available N, P and K showed the opposite trend, and some studies also showed that the content of total nitrogen, available nitrogen and available potassium in artificial grassland soil increased with the increase in recovery years (Sun et al., 2019), which was not consistent with the results of this study, which was due to the heterogeneity of artificial grassland in different recovery years. Compared with severe degradation, the soil organic matter and organic carbon of artificial grassland increased ($p < 0.05$), but with the extension of the recovery period, the trend of the “V" shape was observed in 1-year, 5-year,10-year recovery, the lowest in 5-year recovery, and the overall trend was “high-low-high”. The overall trend of "high-low-high" is consistent with the findings of others (Yang et al., 2015). Compared with severe degradation, the soil pH, water content and bulk density of artificially established grassland will decrease, while high vegetation cover by the time the vegetation community steps into recovery succession will not only reduce evaporation of soil water content but also provide a rich source of organic matter for the soil, further indicating that the improvement of the soil environment is beneficial to the settlement of exotic species, seed germination, root expansion and their nutrient uptake (Wang et al., 2009).

4.3 Differences in microbial characteristics of grasslands under different degradation gradients and different recovery durations

Overall, alpha diversity of bacteria and fungi increased with increasing degradation but decreased with increasing recovery years during recovery. The alpha diversity of bacteria was much higher in artificial grasslands restored for 1–4 years than in those restored by 10–18 years, which are similar to other studies (Gao et al., 2021). Bacterial diversity was higher in the early successional stages of vegetation (4 years) than in the later stages of vegetation succession (8 and 12 years) (Hu et al., 2019). For the degradation process, patch formation significantly increased fungal alpha diversity by approximately 40% (Che et al., 2019). Overall, it is plausible that the significant response of soil bacterial and fungal community alpha diversity to degradation and recovery processes may be influenced in multiple ways. First, soil pH changes frequently during degradation and recovery (Lennon and Houlton, 2017), and an important environmental factor affecting microbial communities is soil pH (Fierer, 2017). Many studies have found that soil pH is negatively correlated with microbial α-diversity during degradation and recovery (Tripathi et al., 2018; Guo et al., 2019). Second, in severely degraded meadows, reduced vegetation cover can accelerate topsoil erosion, increase roughness, and increase light, thus improving the competitiveness of aerobic and photosynthetic autotrophic microorganisms (Lin et al., 2015; Zhang et al., 2017). Bacterial and fungal community structure varies significantly across degradation and recovery processes, with significant differences in microbial communities during the degradation or recovery of alpine grasslands on the Tibetan Plateau (Li et al., 2016; Guo et al., 2019; Zhou et al., 2019). These differences are mainly due to the different vegetation characteristics and soil properties of different degraded and artificial grasslands. Degraded meadows limit plant growth, leading to physical damage to soil structure and nutrient status, which further accelerates soil degradation (Zhou et al., 2019), and alpine meadow degradation will significantly alter bacterial community structure due to reduced availability of microbial substrates as a result of reduced apoplactic inputs (Zhang et al., 2014).

4.4 Differences in plant–soil feedback relationships in grasslands under different degradation gradients and different recovery years

Different soil conditions can have soil-specific effects on plant species (van de Voorde et al., 2011), and changes in soil properties directly affect the direction of plant community succession, providing a theoretical basis for plant–soil feedback (Bever et al., 1997; Bardgett and Van Der Putten, 2014). When studied at the individual plant level, a positive feedback effect value indicates that the plant grows better in the original or the same plant-influenced soil; a negative feedback effect value indicates that the plant has a negative feedback effect in the soil (Baxendale et al., 2014). Similarly, when the plant–soil feedback is positive at a certain stage of plant succession. It means that the plant is growing better at that stage and the soil is in a depleted situation, and *vice versa*. A meta-analysis at the individual species level showed positive plant–soil feedback effects accounting for approximately 28% of the statistics (Kulmatiski et al., 2008). Plant–soil positive feedback can increase the asymmetry of plant growth, leading to the dominance of some plants in a given habitat and the formation of communities dominated by a single plant species, influenced by (1) an increase in available soil nutrients due to plant growth, for example, through plant nitrogen fixation (Chapman et al., 2006), and (2) the accumulation of plant symbionts among the root system (Klironomos, 2002). Most studies have shown that plants in late successional stages are more dependent on interroot symbionts, exhibit greater environmental tolerance, and tend to have a positive plant–soil feedback (Kardol et al., 2006), becomes the dominant species in the community, and gradually become the dominant species in the community. The results of this study showed that in ecosystem multifunctionality, positive feedback was observed in the predegradation period, positive feedback was observed in the moderate to severe degradation for biotic factors, and positive feedback was observed in the moderate degradation for abiotic factors. In the prerecovery stage, plant–soil feedback in ecosystem multifunctionality showed positive feedback, and in the recovery year of 5 years, all three aspects of ecosystem multifunctionality, biotic factors and abiotic factors were positive feedback effects. In the early stage of succession, the preferentially planted plants promote their own growth by decomposing the dead material produced by aboveground plants and the mineralization of nutrients by soil microorganisms while reducing the competitiveness of other plant species in the community, such as the establishment of

Molinia caerulea in the abandoned land where the distribution density of *Calluna vulgaris* is high. The vegetation type gradually changed to grassland (Van der Putten et al., 1993; Berendse, 1994). The positive plant–soil feedback effect is a key factor in early plant changes (Reynolds et al., 2003), and contemporaneous changes in soil properties can have potential long-term effects on plant distribution and productivity (Grman and Suding, 2010; Kulmatiski and Beard, 2011). Plant-soil feedback studies are important for the study of plant community succession, ecosystem multifunctionality and productivity formation and maintenance mechanisms, as well as for theoretical guidance in understanding ecosystem responses to global ecological events, such as climate change and biological invasions.

Negative plant–soil feedback occurs more frequently at the individual species level, accounting for approximately 70% of the included statistics (Kulmatiski et al., 2008). It promotes a balance between the survival states of two plants in a community and, to some extent, species coexistence, with the main influences being (1) nutrient fixation or depletion in the soil, resulting in inadequate supply (Berendse, 1994; de Kroon et al., 2012), (2) accumulation of predators or pathogens under the roots (Van der Putten, 2003) or phytochemical effects of chemicals released by plants (Bais et al., 2003), and (3) some degree of soil carbon aggregation (Ehrenfeld et al., 2005). The results of this study showed that in ecosystem multifunctionality, the late stage of degradation had a negative feedback effect, and biotic factors had a negative feedback effect in mild degradation. The abiotic factors had a negative feedback effect in moderate to severe degradation, and the feedback intensity changed from large to small with the increase in recovery years and the trend from positive to negative feedback. At the recovery year of 10 years in artificial grasslands, the ecosystem multifunctionality, biotic factors and at 10 years of artificial grassland recovery, negative feedback was observed in three aspects: Ecosystem multifunctionality, biotic and abiotic factors. Studies have shown that negative plant–soil feedback effects are generally present in the middle and late stages of semiarid grassland evolution but have less impact on the dominant species (Reinhart, 2012). Some studies have also found that in early successional stages, when an individual plant exhibits a negative feedback effect on itself but a positive feedback effect on other plants growing together within the community, the dominance of this plant is replaced by the coexist plant if other plants exhibit a negative feedback effect on this plant (van de Voorde et al., 2011). During plant community succession, early successional plants exhibit strong negative plant-soil feedback effects on themselves, and if the co-existing species in the community exhibit negative feedback effects on them, this plant species will be replaced by the co-existing species. Thus, negative plant–soil feedback effects can affect plant community structure by suppressing dominant species, reducing the number of most species and decreasing the competitiveness of all species within the community.

5 Conclusion

In this study, plant-soil feedback relationships including ecosystem multifunctionality, biotic and abiotic factors were constructed by analyzing plant, soil and microbial characteristics at seven gradients in the time series of vegetation recovery from mild degradation to 10 years, and the main conclusions were as follows.

1) During the degradation succession of alpine meadows, with the deepening of degradation, above-ground biomass, species diversity index, soil total nitrogen, total phosphorus, available nitrogen, available phosphorus, organic carbon and water content showed a decreasing trend, while soil potassium content showed no significant change trend; soil pH and bulk density showed a significant increase. However, the aboveground biomass showed a decreasing trend with the increase of the recovery years, and the species diversity index showed a "V"-shaped change with the increase of the recovery years, it reached the lowest after 5 years of establishment. Soil total nutrients, organic carbon, pH and bulk density increased, available nutrients decreased, and soil water content was basically unchanged. The alpha diversity of bacterial and fungal communities showed opposite trends between degradation and recovery processes.
2) The positive feedback effect was more than the negative feedback effect in the early stage of degradation, and the feedback effect was stronger with the increase of degradation degree. However, with the increase of the recovery years, the feedback direction changed to negative feedback, and by 10-years of recovery, the feedback was negative. In the process of degradation, ecosystem multifunctionality changed from positive feedback to negative feedback. Biotic factors changed from negative to positive feedback, and abiotic factors had the opposite feedback effect with ecosystem multifunctionality. In the recovery process, there is a trend of positive feedback to negative feedback, and the ecosystem multifunctionality, biotic and abiotic factors all have negative feedback at 10 years of recovery.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

ZH conceived the study, supervised the writing, and revised the manuscript. SY and MT led the writing. LH, ZZ, ML, QR, SH, CT, WJ, and HX contributed sections to the manuscript. ZH provided funding support. All authors read and approved the final submission.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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